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FRUIT-BUD AND FLOWER FORMATION IN THE SULTANINA GRAPE[1]

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INTRODUCTION

THE FRUITING HABIT of the Sultanina[4] grape has required the development of special cultural methods to secure satisfactory crops. These methods, however, are based solely on empirical field observations. An anatomical study of the buds should reveal the differences in fruiting habit of this variety as compared with other varieties and might lead to the development of better cultural practices. The specific objects of this study were to determine (1) the time at which fruit-bud differentiation occurs in the Sultanina, (2) the fruitfulness of the individual buds from the basal to the 20th bud, (3) the rate at which the cluster primordia develop in buds at different positions on the canes, (4) the extent of development of the cluster primordia by the end of the growing season, and (5) the sequence and rate of development of the inflorescences after growth starts in the spring.

REVIEW OF LITERATURE

Former studies of grape-bud anatomy have dealt with the differentiation and early development of the fruit buds and to a less extent with the later stages of flower development. These studies, consisting primarily of field experiments, throw little light on the subject in question. Although Goff[(8)][5] presents considerable data on the initial stages of bud differentiation of different deciduous fruit trees, he simply states that in the grape the embryonic flower is discernible in the autumn prior to blooming. Dorsey[(6)] mentions embryonic grape clusters in the buds before opening and recognizes that each secondary division of the embryonic

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[4] Also called Thompson Seedless in California, and Sultana in Australia.

[5] Superscript numbers in parentheses refer to "Literature Cited" at end of this paper.

cluster occupies a position axillary to a bract. In his textbook Perold,[12] quoting from Müller-Thurgau, points out that the first cluster is initiated about the middle of June, the second cluster about July 1, and that no further initiation occurs in the buds after August 1. Partridge[10] places the time of fruit-bud initiation at midsummer. According to him, the primordium remains a mass of heavily nucleated cells until spring, when the cluster develops after growth starts. Snyder[14] shows that differentiation in the Concord begins early in June and continues in the newly forming buds throughout the growing season. Barnard[1] and Barnard and Thomas,[3] studying Sultana in Australia, discuss the problem rather extensively. Their results, however, are concerned primarily with the distribution of fruit buds on the canes and with the percentage of fruitful buds in a given location.

METHODS USED

The materials studied were collected from the experiment vineyards of the University Farm, Davis, California. Although the soil and vines were fairly uniform, there was some variation in the size and length of individual canes on each vine. This reflected itself as variations in the sizes of the primordial clusters of buds collected on the same date and taken from the same position on different canes.

The collections of buds were made on June 7, 19, and 29; July 11 and 22; August 1 and 22; October 6; and December 5, 1933; and on March 4, 1934. A collection consists of one cane taken from each of fifteen vines. All buds of a given node were placed together and treated as one lot—fifteen buds, accordingly, for each node. All the buds on the canes for the first three collections were used. After the third collection only every other bud was taken above the 4th bud. Since, furthermore, canes of more than twenty buds are rarely retained in the pruning of this variety, no buds were taken from beyond the 20th node.

One week after the last collection of buds (that of March 4, 1934), the first buds began to open. Opening continued about fifteen days. Since the date at which growth begins changes considerably from year to year, it was thought best to include the approximate stage of development of the flower parts by average length measurements of the clusters (table 3) in addition to the date of collection. The dates of the collections of the inflorescences serve to indicate the rate of development of the floral parts. The buds were killed and fixed in Karpechenko's solution. After being washed with tap water, they were passed through alcoholic solutions of increasing concentration up to the 70 per cent solution in which they were stored until used. To facilitate penetration of the killing and fixing

solution, the hairy bud scales were removed, and the buds were put under partial vacuum. Sinking of the buds in the solution was taken to indicate satisfactory penetration.

The buds were then dehydrated with alcohol, cleared in xylene, and infiltrated with and embedded in paraffin. Since the bud scales are rather hard to cut, the embedded buds were soaked in water for one or two weeks before sectioning. A disinfectant was added to the soaking water to prevent the growth of destructive organisms. Delafield's haematoxylin was used for staining, with safranin as a counter stain.

THE MORPHOLOGY OF THE BUD, CLUSTER, AND TENDRIL

Grape buds are generally classified as mixed buds; that is, both leaves and fruit develop from the same bud. They form in the axils of the leaves. The lower buds originate in the axil of the leaf primordia in the previous year's buds (*A* in fig. 4, plate 1, and in fig. 7, plate 2). Inside the scales covering the bud is the growing point with its leaf primordia. Each leaf has two stipules that Barnard[3] calls stipular scales, as large as the leaf primordium or larger. Since they lignify very early, they stain red with safranin and contain many tannin bodies. These stipular scales can be seen on both sides of the base of the petiole of the leaves near the distal end of a growing shoot, whereas only stipular scars remain beside the petioles of the older leaves toward the basal end of a shoot. The arrangement of leaf primordia is distichous. Longitudinal sections through the leaf primordia are shown in figure 4, plate 1 and figure 7, plate 2. Sections at other angles (fig. 8) show only stipular scales. The leaf is initiated as a pointed protuberance from the growing point of the bud (*L* in fig. 2, plate 1, and in figs. 7 and 12, plate 2).

The first initiation of clusters was visible the first week of June. The growing point becomes bilobed; and one of the parts as indicated at *C* in figures 1–6, plate 1, becomes the initial of a cluster, whereas the other continues to be the growing point. It is rather easy to detect whether the new differentiating apex is to be a leaf or cluster primordium, since the leaf forms from a narrow, pointed primordium (*L* in fig. 2, plate 1 and in figs. 7 and 12, plate 2) whereas a cluster of primordium is rather blunt and broad (*C* in figs. 1–6, plate 1). The cluster primordium is always opposite a leaf (*L* and *C* in fig. 2, plate 1 and in fig. 12, plate 2). Thus only sections that are cut in the plane with the growing point and the primordial cluster and leaves will show both these primordia (fig. 4, plate 1; fig. 7, plate 2; and fig. 17, plate 3). Median sections in other planes will show only stipular scales. Nonmedian sections may show clusters (fig. 8, plate 2) and stipular scales but no leaf primordia.

Snyder[14] states that leaf and cluster primordia are alike in the initial stages. Even in this earliest stage of differentiation, however, as figures 1 and 2 (plate 1) will show, the pointed leaf primordium *L* is rather easily distinguished from the blunt cluster primordium *C*. Barnard[1] states that the new organic apex of the bud arises from the apical tissue subtended by a leaf; he interprets this as a sympodial growth, so that the cluster primordium would be terminal. The sympodial origin of the cluster is given general support in the textbooks on viticulture. The rather equal division of the growing point occurring in some buds, the absence of a subtending leaf or stipular scale, and the alternate arrangement of leaves support this idea. A close examination of the growing points of our material revealed, however, that the division of the growing apex to form the cluster primordium in most buds is not equal, which suggests that the cluster may be a lateral rather than a terminal initiation. Further data will be required to support this view.

Goebel[7] states that he does not believe that tendrils are "formed as evident continuations of the internode below them and then only gradually pushed to the side by the stronger growth of the uppermost axillary shoot." Having usually found the tendril primordia situated distinctly laterally on the growing axis, he states: "They either from the first have the leaf-opposed position of the mature condition or . . . proceed from the apex of the axis itself through its unequal division." If the tendrils are not terminal and if, as Goebel points out, they are phyletically derived from inflorescences, it is not unreasonable to accept the possibility of the lateral initiation of cluster primordia, especially since there are many gradations between true cluster and true tendril, a fact that supports their homology. To us this conception appears more tenable than to accept the cluster as terminal and consider it a sympodial growth.

Field studies show that the tendrils occur in a leaf-opposed position the same as the clusters. They are never found below the clusters on the shoot. A tendril primordium (*T*) is shown in figure 9, plate 2, and figure 16, plate 3.

The divisions of the primordial cluster are first indicated by the appearance of bracts subtending the cluster branches (*B* in figs. 4 and 5, plate 1; and in fig. 11, plate 2). The first bract usually arises from the side of the cluster primordium farthest from the growing point. The first bracts were discernible a week or ten days after cluster initiation. By the middle of July, when the increase in size of the cluster primordia slows down, the lateral surface of the primordial clusters is crowded with branches, each subtended by a bract (fig. 9, plate 2, and fig. 18, plate 3). Although growing less rapidly as the season proceeds, the

cluster primordia divide again and again to give rise to secondary and tertiary cluster branches. When the buds open in spring, they are still in primordial form. The apical part of many clusters is still an undivided mass of meristematic tissue (figs. 16, 17, and 18, in plate 3). As shown in the apical part, *U* of figure 20, plate 4, differentiation continues just before and for a short time after the buds open. After the leafing out, however, it is soon superseded by the very rapid initiations of the flower parts.

THE DEVELOPMENT OF FRUITFUL BUDS

The number of buds found to be fruitful for each position on the fifteen canes taken at each collection is shown in table 1. The columns, except the one at the left that indicates position, represent the fruitful buds

TABLE 1

NUMBER OF BUDS FOUND TO BE FRUITFUL OF THE FIFTEEN COLLECTED FROM VARIOUS POSITIONS ON THE CANES

Position of buds on cane	Date of collection								
	June 7, 1933	June 19, 1933	June 29, 1933	July 11, 1933	July 22, 1933	August 1, 1933	August 22, 1933	December 5, 1933	March 4, 1934
Basal	3	3	5	8	7	8	7	8	9
1	4	5	6	9	9	9	10	8	9
2	4	5	7	11	13	13	13	12	13
3	2	8	8	11	14	15	14	13	14
4	3	6	10	12	14	15	15	15	15
5	3	6	12	14	..	..	..	..	..
6	1	6	11	13	15	15	15	14	15
7	1	5	10	..	..	..	..	..	..
8	1	6	8	13	13	14	14	13	14
9	..	4	8	..	..	..	..	..	..
10	..	4	6	10	12	15	13	15	14
11	..	2	4	..	..	..	..	..	..
12	..	3	4	10	11	13	14	14	15
13	..	2	4	..	..	..	..	..	..
14	..	2	3	7	13	12	12	14	14
15	..	1	2	..	..	..	..	..	..
16	..	..	..	5	10	11	12	11	13
17	..	..	..	..	..	..	..	..	..
18	..	..	..	5	9	9	10	13	14
19	..	..	..	..	..	..	..	..	..
20	..	..	..	4	8	8	9	12	12

collected on the date shown at the top of the column. The number of differentiated buds increases rather rapidly as the season proceeds, up to about August 1. After this date there is a slow but continual increase in the fruitfulness of the buds above bud 12.

The buds on the basal end of a cane differentiate first. As the season advances, however, the maximum differentiation is soon shifted to the

region between the 4th and 12th buds of the cane, where it remains. The figures further indicate that the basal and first buds are the least fruitful of the buds on the part of the canes studied. The fruitfulness of the buds increased up to the 4th bud; from the 4th to the 12th buds it was about the same; from the 12th bud upwards it decreased. This observation closely agrees with crop records at Davis, which indicate that the total weight of crop, weight of cluster, and average crop per node increase from the basal up to the 6th bud. Between the 6th and 10th buds the figures remain about the same, whereas beyond the 10th bud they decline. The basal buds were 45 to 50 per cent fruitful, but the 6th to the 10th buds inclusive were 80 to 100 per cent fruitful. Keffer[9] reports

TABLE 2

A Key to the Photomicrographs, Showing the Stage of Development of the Buds at Different Positions on the Canes

Date of collection	Basal node	1st node	4th node	6th node	10th node	14th node	20th node
June 7, 1933	..	..	..	1*	..	..	..
June 19, 1933	..	..	..	3	2	..	..
June 29, 1933	..	..	..	5	4	..	..
July 11, 1933	6	7	8	9	10	11	12
July 22, 1933	..	..	..	13	..	..	..
August 22, 1933	..	..	..	14	..	..	15
March 4, 1934	..	16	..	17	..	..	18

* These numbers refer to the figure numbers of buds appearing in plates 1 to 3 inclusive.

similar results. He states: "The first buds formed in the spring are less well developed than the following buds; and . . . toward the end of the season buds on the distal end of the cane are not so well developed as those formed earlier in the season."

Table 1 shows the course of differentiation of the buds at a given node on the canes throughout the season. The lower buds on the cane were the first to show cluster initiation. In the buds farther up, other conditions being favorable, cluster initiation more or less paralleled the development of the shoot; that is, when the shoot had attained a given state of development, the buds began to show cluster initiation. The buds on the lower part (bud 4) of the cane reached maximum development before those in the midportion (bud 12) of the cane, the reason being the difference in the time of their formation.

The photomicrographs show the difference in size of primordial clusters at the different positions on the canes and at the different dates of collection. In order to show representative development, the specimens for the photomicrographs were so chosen (table 2) that the differentiation of a bud at a given position could be followed through the season,

as well as the differences in size of the primordial clusters in the buds at different positions on the canes for a given date. For the first purpose the 6th bud was selected and followed from the earliest collection showing cluster initiation until the next spring, to show the stages of growth of the primordial cluster. For the latter purpose the canes that were collected on July 11 were chosen. Such an arrangement of the buds reveals that for the 6th bud, the increase in size of the primordial cluster is rather rapid until the middle of July, then slows down gradually; after August the increase is relatively slow (figs. 1, 3, and 5 in plate 1; 9 in plate 2; 13, 14, and 17 in plate 3). The buds farther up on the cane, which developed later, were also later in differentiation and followed the 6th bud in this respect at each date of collection until after August 1. The most rapid increase in differentiation in these buds also came somewhat later in the season than that of the 6th bud. The uppermost buds examined were the latest in development in all respects. Not until the end of the season did their development begin to equal that of the 6th bud. In the upper buds of the canes, however, the development never did attain equality. A comparison of the 20th bud on the August 22, 1933 (fig. 15, plate 3) and March 4, 1934 (fig. 18, plate 3) collections will show that there was a marked increase in size during this period. The great increase in size, however, occurred prior to the October 6 collection. There was no perceptible change between the December 5 and March 4 collections.

Since the differentiation of buds on a cane starts from the base and proceeds upwards, a difference in the size of the primordial clusters in the same direction would be expected. An examination of the buds collected on July 11, 1933 (fig. 6, plate 1, and figs. 7–12, plate 2), shows that, although the first three buds are earlier in time of differentiation than the 4th to 10th buds, their primordial clusters are smaller. The 4th to 8th buds have the largest primordial clusters. Beyond the 8th bud the size of the primordial clusters decreased gradually, until in the 20th bud only the beginning of differentiation was visible. The trend of development in the buds of the August 22, 1933, collection was similar to that described above. The cluster primordia in the basal buds were smaller than those of the first and second buds. Their size increased gradually up to the 4th bud, became about constant from the 4th to the 10th bud, and above the 10th bud decreased again. By the time the buds were ready to open in spring these differences diminished. The differences that persisted, however, though small, were in the same direction as in the younger buds (figs. 16, 17, and 18, plate 3). The findings of Colby and Tucker[6] with Concord closely agree with these figures.

SEQUENCE AND RATE OF DEVELOPMENT OF THE INFLORESCENCE

Our observations on the sequence of the development of the floral parts of *Vitis* agree with those of Sartorius,[13] Baranov,[2] and others—namely, that it is regular. The calyx, corolla, stamens, and pistil are differentiated in the order named. Each flower primordium pushes out from the axis, to which it is attached, as an undifferentiated, rather roundish mass of meristematic tissue (*Uf* in fig. 20, plate 4). The calyx (*S* in figs. 20 and 21, plate 4) first appears as a protuberance on either side of this meristematic surface in the longitudinal sections. The initiation of the corolla (*P* in fig. 21, plate 4) primordium follows the calyx in similar manner. As the calyx grows, the lobes bend inward, come in contact with each other, and give the impression of a coalescence. Snyder,[14] having observed a similar condition in *labrusca*, reports the case as an actual coalescence, while Sartorius[13] states that the end cells of the sepals are simply held together with a sticky substance in *Vitis vinifera*. Barnard and Thomas[3] could not find this condition in Sultanina. As the corolla lobes grow upward they separate the sepals (figs. 22 and 23, plate 4). During their upward growth the petals bend inward and come in contact with each other to form the so-called calyptra (*P* in fig. 22, plate 4).

According to Snyder[14] extensive cell division occurs in the parts of the petals that touch, and a considerable mass of what he terms "callus" is formed at their tips. This was not the case in our material. Usually the epidermis of petals has an irregular outline, and the cell walls bulge out. When the petals come together, the projecting cells of one intermesh into those of the other, and thus interlock the petals. This agrees with the findings of Sartorius.[13] The red-staining cuticle layer clearly shows the line of meshing; and the fact that the petals separate from each other at the base along this line when the calyptra is shed indicates the lack of actual union of the cells. Snyder's mass of "callus" cells is, in fact, a portion of the posterior lobe, which in sectioning has been left in the same plane with the two lateral lobes. The same red-staining substance aids in identifying the cells as belonging to the epidermal tissue. In this case the petal tissue is cut tangentially.

Before the calyptra is completely formed, the primordia of the stamens are discernible as definite lobes (*St* in figs. 21 and 22, plate 4).

The primordia of the carpels appear soon after the meshing of the petals (*Cp* in fig. 23, plate 4). They arise from the meristematic apex in a manner similar to the other parts. At this stage of development the stamens show no evidence of differentiation into anthers and filaments.

Figure 24, plate 4, shows the further development of the carpels; the stamens show the differentiation into anthers (*An*) and filaments (*F*). The primary sporogenous tissue is discernible in the anthers.

The further increase in size of carpels is associated with the development of the ovules. The ovules, their structures, and the sequence of their development were described in some detail by Berlese[4] as early as 1892. His descriptions have been confirmed and expanded by Sartorius,[13] Baranov,[2] and others. The sequence and rate of development of the structures of the ovule are described in greater detail by the latter workers. We have attempted to correlate the development of the individual flower and its parts with cluster size and time (table 3). The

TABLE 3

LENGTH OF CLUSTER AND DEVELOPMENT OF FLOWER PARTS ON THE DATES ON WHICH THE INFLORESCENCES WERE COLLECTED

Length of cluster, inches	Date* of collection	Figure numbers (plates 4 and 5) showing average development for each group
¼– 1	March 18	19, 20
1 – 2	April 1	19, 21
2½	April 8	22
2½– 3	April 13	23
3 – 4	April 21	24, 25
4 – 5	April 25	26, 27
7 –10	May 1	28, 29, 30

* Vine development was almost three weeks earlier than usual during this period of development in the 1934 season.

rate of development of both the flowers and the cluster is influenced, however, by climatic and seasonal conditions.

Although the number of carpels in *Vitis* is two, it is not unusual to find three. Two ovules arise in each carpel. The ovule primordium (*Nu* in fig. 24, plate 4) first appears as a protuberance. It continues to increase in size until it completely occupies the ovarian cavity (fig. 25, plate 5). The placentation is axile. A ring of tissue, arising near the tip of the nucellar tissue, forms the inner integument (*I* in fig. 26, plate 5), which in turn is followed by the formation of a second ring of tissue outside the first, which develops into the outer integument (*O* in fig. 27, plate 5). Approximately a week after the outer integument is initiated, the macrospore mother cell has passed through the second meiotic division to form a tetrad. Since *Vitis* species have anatropous ovules, these structures must move through a considerable arc (figs. 26–29, plate 5). This growth begins soon after the inner integumentary ring becomes dis-

cernible (figs. 26 and 27, plate 5). At this stage the macrospore mother cell can be seen. The bending of the funiculus continues until the ovule tip is directed downward toward the placenta (fig. 29, plate 5). The inner integument has now grown to enclose the nucellus entirely, leaving only the micropylar opening at the lower end. In the Sultanina the development of the inner integument is abnormal, so that its tubular tip is distorted and presses against the ovary wall toward the funiculus (fig. 30, plate 5). Pearson,[11] who observed a similar condition, states that the outer integument is abnormally short. By the time the stage of development shown in figure 30 is reached, the egg cell is ready for fertilization.

During these stages of megasporangial development the primary sporogenous tissue in the anthers divides to form microspore mother cells. About the time the first integumentary ring appears in the ovule, the microspore mother cells enter the prophase of the first meiotic division. At the stage of development shown in figures 28 and 29 (plate 5) each member of a tetrad rounds off and separates to form a microspore. By the time the ovule has reached the stage of development shown in figure 30, the microspores have become mature.

SUMMARY

A histological study of the Sultanina was undertaken in order to determine the time of differentiation of the fruit buds and the course of development of the primordia.

Cluster primordia begin to be initiated during the first week of June. They appear as blunt, rather broad outgrowths of the growing point of the bud. The leaf primordium, on the contrary, appears as a pointed outgrowth from the growing point and is readily distinguished from the cluster primordium.

The most productive part of the canes is the portion between the 4th and 12th buds. The basal and distal buds on a cane are the least productive. The primordial clusters in the basal and apical buds of the canes do not become so large as those in the buds in the middle of the canes.

The differentiated cluster primordia increase rapidly in size during the early season and then slow down. There is no perceptible increase during the dormant period.

The formation of a bract is the first indication of the division of the primordial cluster. Bract formation is discernible a week or 10 days after cluster initiation. Lateral cluster branches arise in the axils of these bracts. By the end of the season the lateral surface of the primordial cluster is a mass of bracts and branch primordia.

Tendril primordia form later in the season than primordia of the clusters.

The development of the flower is regular. The parts follow each other in rapid succession in their development. Six to seven weeks after leafing out, the development of parts is complete.

LITERATURE CITED

[1] Barnard, C.
1932. Fruit bud studies: 1. The Sultana. An analysis of the distribution and behavior of the buds of the Sultana vine, together with an account of the differentiation and development of the fruit bud. Jour. Council Sci. and Indus. Research 5:47–52.

[2] Baranov, P.
1927. Zur Morphologie und Embryologie der Weinrebe. Ber. Deut. Bot. Gesell. 45:97–114.

[3] Barnard, C., and J. E. Thomas.
1933. Fruit bud studies: II. The Sultana. Differentiation and development of the fruit buds. Jour. Council Sci. and Indus. Research (Australia) 6: 285–94.

[4] Berlese, A. N.
1892. Studi sulla forma, strutta, e sviluppo del seme nelle Ampelidae. Malpighia. 6:293.

[5] Colby, D. S., and L. R. Tucker.
1926. Growth and fruit production studies in the grape. Amer. Soc. Hort. Sci. Proc. 25:210–16.

[6] Dorsey, M. J.
1914. Pollen development in the grape with special reference to sterility. Minnesota Agr. Exp. Sta. Bul. 144:1–49.

[7] Goebel, K.
1905. Organography of plants. 707 p. (See specifically Part II, English ed. Oxford, Clarendon Press. p. 435.)

[8] Goff, E. S.
1901. Investigations of flower buds. Wisconsin Agr. Exp. Sta. Rept. 18:304–16.

[9] Keffer, A. C.
1906. The fruiting habit of the grape. Tennessee Agr. Exp. Sta. Bul. 77:36–46.

[10] Partridge, N. L.
1929. Relation of blossom formation in the Concord grape to current season conditions. Amer. Soc. Hort. Sci. Proc. 26:261–64.

[11] Pearson, Helen M.
1932. Parthenocarpy and seed abortion in *Vitis vinifera*. Amer. Soc. Hort. Sci. Proc. 28:169–75.

[12] Perold, A. I.
1927. A treatise on viticulture. 696 p. (See specifically p. 38.) The Macmillan Co., New York.

[13] Sartorius, O.
1926. Zur Entwicklung und Physiologie der Rebblüte. Angew. Bot. 8:29–89.

[14] Snyder, J. C.
1933. Flower bud formation in the Concord grape. Bot. Gaz. 94:771–79.

EXPLANATION OF PLATES

PLATE 1

Photomicrographs of longitudinal sections through the buds from the collections of June 7, 19, 29, and July 11. (× 26.) Compare figures 1, 3, and 5 with figure 9, plate 2, and with figures 13, 14, and 17 of plate 3, to note the influence of time on stage of development; and compare figure 6 with figures 7–12, plate 2, to note the influence of position of the bud on the stage of development of the cluster primordium.

Fig. 1.—Bud from the 6th node, June 7 collection. *C*, Early stage in the development of the cluster primordium. *L*, Leaf initial.

Fig. 2.—Bud from the 10th node, June 19 collection. *C*, Early stage in the development of the cluster primordium. *L*, Early stage of leaf development.

Fig. 3.—Bud from the 6th node, June 19 collection. *C*, Cluster primordium. *A*, Buds in the axils of the primordial leaves.

Fig. 4.—Bud from the 10th node, June 29 collection. C_1, Early stage in the development of the upper (second) cluster primordium. *C*, Lower (first) cluster primordium. *B*, Initial stage of a bract on the primordial cluster. *A*, Buds in the axils of the primordial leaves.

Fig. 5.—Bud from the 6th node, June 29 collection. *C*, Cluster primordium. *B*, Initial stage of a bract on the primordial cluster.

Fig. 6.—Bud from the basal node, July 11 collection. *C*, Cluster primordium.

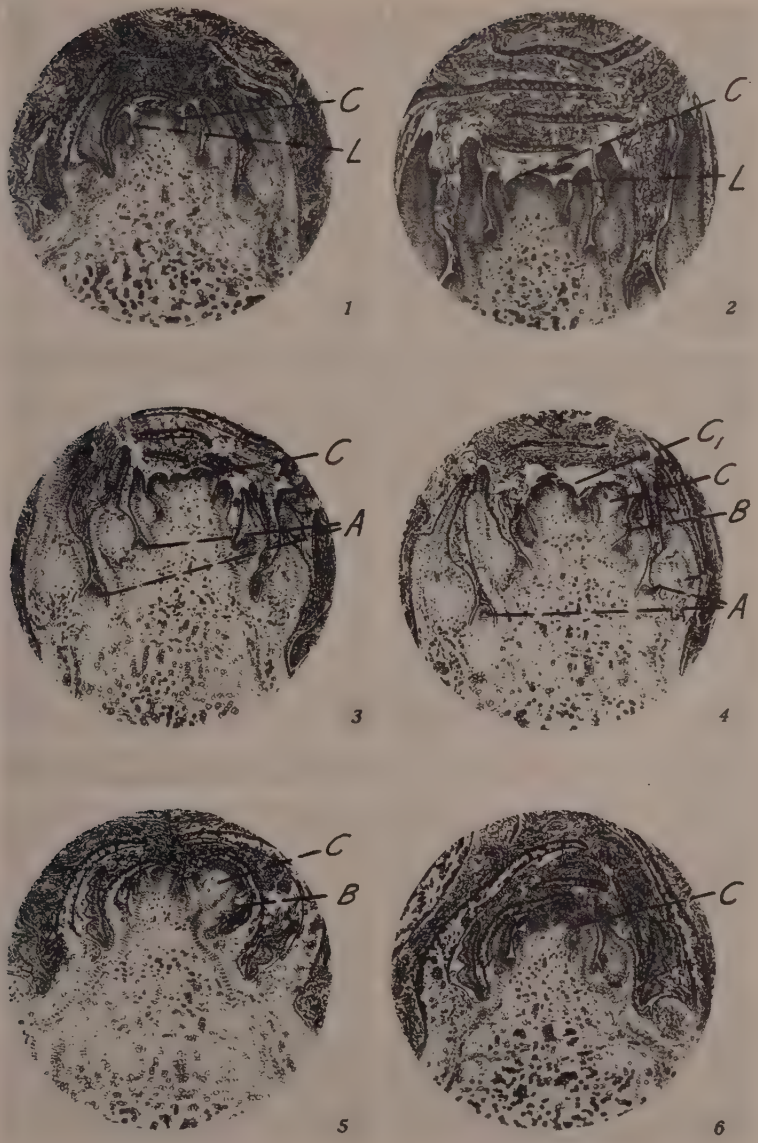

C
L
1
C
L
2
C
A
3
C1
C
B
A
4
C
B
5
C
6

PLATE 2

Photomicrographs of longitudinal sections through buds from different positions on the canes from the collection of July 11. (× 26.) Compare figures 7–12 with figure 6, plate 1.

Fig. 7.—Bud from the 1st node. *C*, Cluster primordium. *L*, Early stage of leaf development. *A*, Buds in the axils of the primordial leaves.

Fig. 8.—Bud from the 4th node. *C*, Cluster primordium. *Cb*, Branches on the cluster primordium.

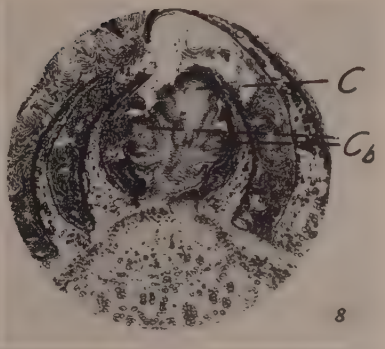
Fig. 9.—Bud from the 6th node. *C*, Cluster primordium. *Cb*, Branch on the cluster primordium. *T*, Early stage of development of a tendril. B_1, Bract on the branch primordium. *B*, Bract subtending the branch primordium.

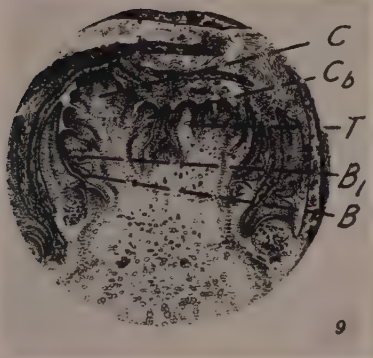
Fig. 10.—Bud from the 10th node. *C*, Cluster primordium. *B*, Bract subtending the branch primordium.

Fig. 11.—Bud from the 14th node. *C*, Cluster primordium. *B*, Initial stage of a bract on the primordial cluster.

Fig. 12.—Bud from the 20th node. *C*, Cluster primordium. *L*, Early stage of leaf development.


C
L
A
7


C
C_b
8


C
C_b
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B_1
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C
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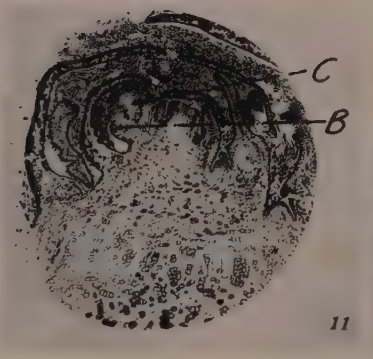
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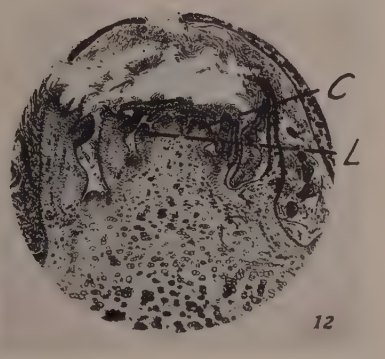
C
L
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PLATE 3

Photomicrographs of longitudinal sections through buds from the collections of July 22, August 22, and March 4. (×26.)

Fig. 13.—Bud from the 6th node, July 22 collection. C_1, Upper cluster primordium. *C*, Lower cluster primordium. *Cb*, Branch on the cluster primordium. *B*, Bract subtending the branch primordium.

Fig. 14.—Bud from the 6th node, August 22 collection. *C*, Cluster primordium.

Fig. 15.—Bud from the 20th node, August 22 collection. *C*, Cluster primordium. *B*, Bract subtending the branch primordium.

Fig. 16.—Bud from the 1st node, March 4 collection. *C*, Cluster primordium. *T*, Early stage of development of a tendril.

Fig. 17.—Bud from the 6th node, March 4 collection. *C*, Cluster primordium. *Cb*, Branch on the cluster primordium. *B*, Bract subtending a branch primordium.

Fig. 18.—Bud from the 20th node, March 4 collection. *C*, Cluster primordium. *Cb*, Branch on the cluster primordium. B_1, Bract on the branch primordium. *B*, Bract subtending a branch primordium.

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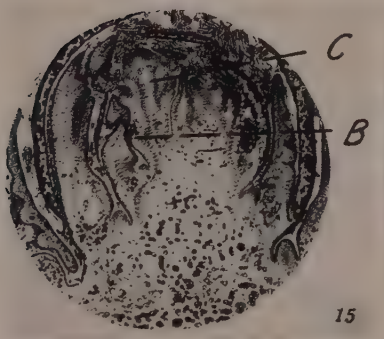

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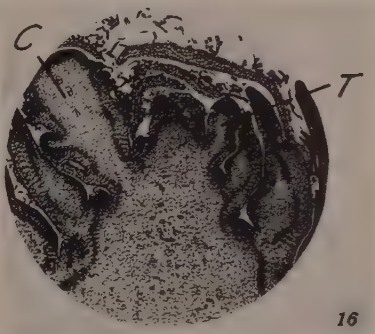

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PLATE 4

Photomicrographs of longitudinal sections through cluster branches, showing the initiation and development of the flower parts.

Fig. 19.—Cluster branch about two weeks after leafing out. (×26.) *K*, The coming together of the petals to form the calyptra. *B*, Bract subtending an individual flower. *R*, The coming together of the sepals, which occurs early in the development of the flower parts.

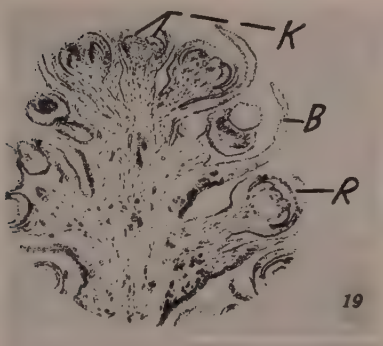
Fig. 20.—Cluster branch about one week after leafing out. (×100.) *U*, Undifferentiated mass of meristematic tissue from which several more flowers may arise. *Uf*, Undifferentiated mass of meristematic tissue from which the flower parts will arise. *S*, Beginning of calyx differentiation.

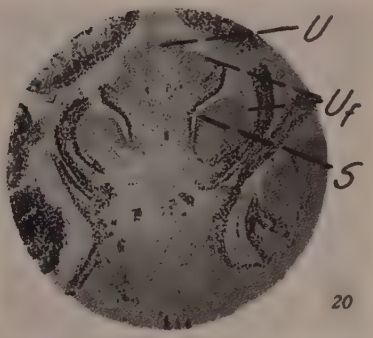
Fig. 21.—A flower about two weeks after leafing out. (×100.) *S*, The lower line shows an early stage of calyx development, while the upper line points to a later stage of development of the calyx. *P*, Early stage of corolla development. *St*, Initiation of stamen differentiation.

Fig. 22.—A flower about three weeks after leafing out. (×100.) *S*, Calyx; the sepals still appear coalesced. *P*, Corolla; the petals are coming together above to form the calyptra. *St*, Initiation of stamen development.

Fig. 23.—A flower three to four weeks after leafing out. (×100.) *S*, Calyx. *P*, Corolla. *St*, Stamen. *Cp*, Initiation of carpel development.

Fig. 24.—A flower about four weeks after leafing out. (×100.) *P*, Calyx. *S*, Corolla. *An*, Anther. *Cp*, Carpel. *F*, Filament. *Nu*, Nucellus.


K
B
R
19


U
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S
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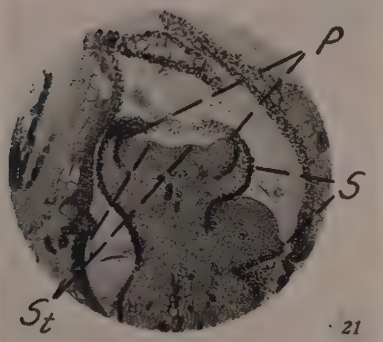
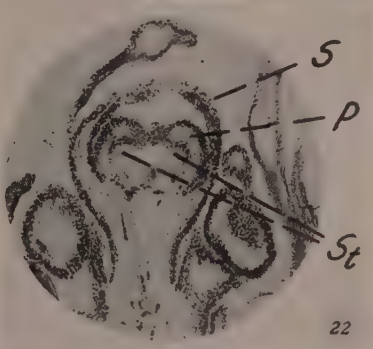

P
S
St
21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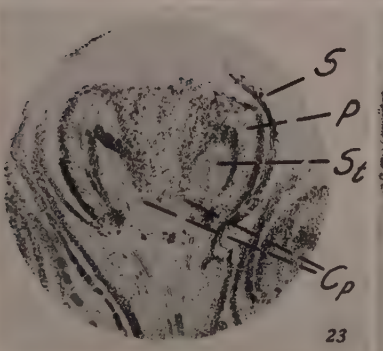
S
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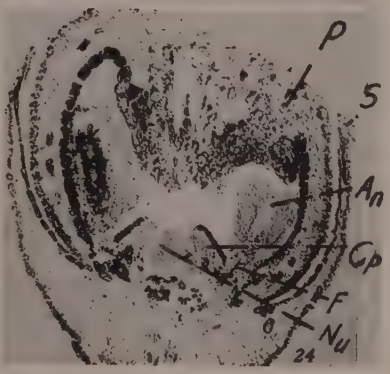

P
S
An
Cp
f
Nu
24

PLATE 5

Photomicrographs of longitudinal sections through flowers, showing the development of the parts. (× 100.)

Fig. 25.—A flower four to five weeks after leafing out. *Ov*, Ovary. *Nu*, Nucellus. *F*, Filament.

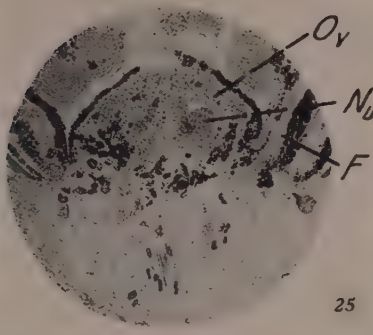
Fig. 26.—A flower several days later than that shown in figure 25. *Nu*, Nucellus. *I*, Initiation of the inner integument.

Fig. 27.—A flower about a week later than of figure 25. *X*, Early stage in the development of the style. *O*, Outer integument. *I*, Inner integument. *Nu*, Nucellus. (The bending of the funiculus is first discernible at this stage.)

Fig. 28.—A flower several days later than that of figure 27. The ovule is pointing downward, and its parts have advanced in development. *X*, Style. *O*, Outer integument. *Nu*, Nucellus. *I*, Inner integument.

Fig. 29.—A flower five to six weeks after leafing out. The flower parts are approaching maturity.

Fig. 30.—The mature megasporangium. The inner integuments elongate abnormally, so that the micropyle may be contorted. *M*, Micropyle. *O*, Outer integument. *I*, Inner integument.



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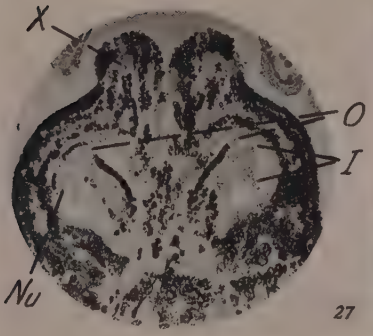

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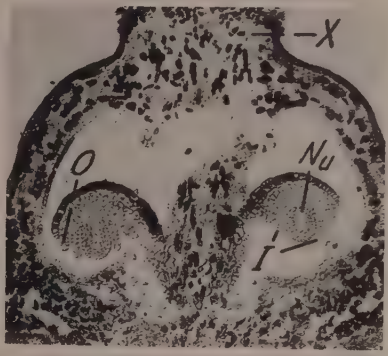

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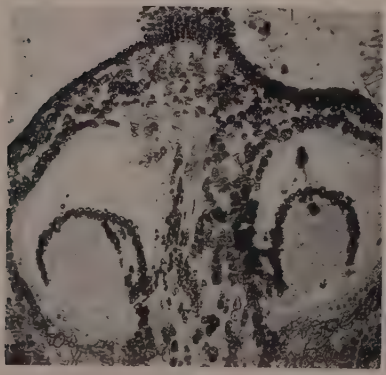

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MORPHOLOGY OF THE FLOWER AND FRUIT OF THE LOQUAT

ROBERT M. SMOCK

MORPHOLOGY OF THE FLOWER AND FRUIT OF THE LOQUAT[1, 2]

ROBERT M. SMOCK[3]

INTRODUCTION

THE LOQUAT (*Eriobotrya japonica*), indigenous to China, is grown more or less extensively in California, Florida, and the Gulf States. *Eriobotrya japonica* is in the family Rosaceae, subfamily Pomoideae. The Greek translation of *Eriobotrya*—"woolly inflorescence"—well depicts the extremely hairy condition of buds, flowers, fruits, and leaves. In China the loquat is called "rush orange."

Bailey[(1)][4] describes the tree as small and evergreen with leaves "elliptical to oblong-ovate, nearly sessile, and remotely toothed." The small, white flowers are borne in woolly panicles 4 to 7 inches long (fig. 1). Development of the panicle is acropetal. The flower panicles are terminal on the current season's growth. Growth extension occurs from terminal leaf buds on nonfruiting branches and from the distal lateral leaf bud on fruiting branches. The flowers are pentamerous, and each of the five carpels contains two ovules; ordinarily only one to eight seeds develop. Seedless varieties, though sometimes reported, are of no commercial importance. Condit[(2)] has described climatic adaptations, culture, and varieties of the loquat.

This paper presents the results of a study of the morphology of the loquat flower and fruit.

MATERIALS AND METHODS

Loquat buds, flowers, and fruits were collected at weekly intervals during the 1934–35 season from a tree of the Advance variety on the University Farm at Davis, California.

The extremely hairy condition of the buds made paraffin sectioning difficult. Celloidin, double infiltration as described by De Zeeuw,[(3)] butyl alcohol, and glycerine-butyl alcohol were therefore employed as softening agents in attempts to avoid tearing of sections. Although fairly satisfactory results were obtained with celloidin-imbedded material, the

[1] Received for publication November 24, 1936.

[2] The author wishes to express his appreciation for the help and criticism of Dr. Warren P. Tufts, who suggested the problem.

[3] Junior Pomologist in the Experiment Station.

[4] Superscript numbers in parentheses refer to "Literature Cited" at the end of this paper.

method adopted was to kill bud samples in formalin-acetic-alcohol fixative and then expose them for several hours to 5 per cent hydrofluoric acid in 70 per cent alcohol.

Flowers and fruits were scraped practically free of hairs with a scalpel before being exposed to the killing agent. Soaking of the paraffin blocks

Fig. 1.—Panicle of loquat flowers at anthesis.

in water in an oven at 30° centigrade for several weeks facilitated sectioning.

Medium Flemming's killing agent and Navashin's modification of Karpechenko's were employed for flowers used in macrosporogenesis studies. The former proved more satisfactory. Delafield's haematoxylin stain was used for most of the material; gentian violet or Haidenhain's

haematoxylin for more delicate work. Although sections were usually cut 14 microns thick, flower sections used in macrosporogenesis studies were 8 microns in thickness.

FLOWER-BUD DEVELOPMENT

The period of flower-bud differentiation and of flowering is extended. Buds showing early stages of flower-bud development were collected as late as November 6. Buds were not collected early enough in 1934 to indicate at what time of year the first signs of differentiation began.

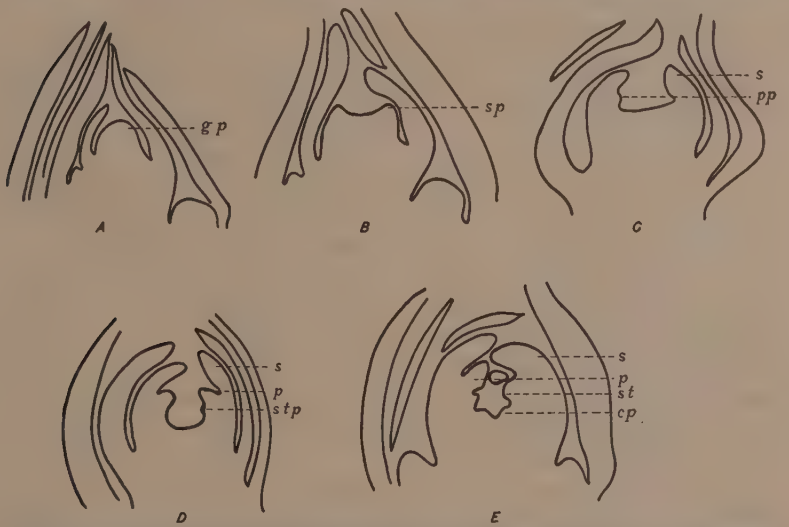


Fig. 2.—Sections showing development of typical loquat flower bud. The parts are: *gp*, growing point; *s*, sepal; *p*, petal; *st*, stamen; *sp*, sepal primordium; *pp*, petal primordium; *stp*, stamen primordium; *cp*, carpel primordium.

Buds that possessed flower primordia were tagged on October 17; these were in full bloom by December 28. The period of full bloom for the whole tree was from October 17 to February 1.

The first discernible sign of flower-bud differentiation is a distinct, blunt protuberance. As a result of a rapid multiplication of the cells at the outer edge of this protuberance, a slightly elevated ridge appears (fig. 2, *A*). Very soon cell division at five points around the circumference of this ridge results in the formation of the sepal primordia (fig. 2, *B*). The torus, meanwhile, has been undergoing rapid development, especially basal to the calyx. As a result of this toral growth the rapidly forming sepals are elevated. They develop quickly, and their apices grow towards each other so as to enclose the distal portions of the carpels. The

sepals as well as all of the exposed toral surfaces are densely covered with long epidermal hairs.

Very soon after the sepal primordia develop, those of the petals appear, arising in a whorl alternating with the sepals (fig. 2, *C*). Growth of the petals and sepals continues, and soon they cover over in "hood" fashion the cup-shaped torus (figs. 2, *D* and 2, *E*). Each petal is constricted at the point of divergence from the torus.

Shortly after the petal primordia appear, those of the stamens develop in three cycles around the torus directly inside the petals. The outer cycle of stamens develops first; then the middle, and finally the inner cycle is initiated. The innermost and middle cycles of stamen primordia number five each, while those of the outer consist of ten, there usually being twenty stamens in all. The stamen cycles are too close together to be easily differentiated from one another by the naked eye.

The five carpel primordia are formed soon after the inner cycle of stamen primordia is developed. They arise from the cup-shaped receptacle just basal to the inner cycle of stamens and some distance from the center of the torus (that is, at the apex of the pedicel). Infolding of the carpel edges takes place very early in carpel development. Carpel growth proceeds rapidly, and soon adnation of the lower portions of the carpels is so complete that one cannot discern the infolded edges, which are clearly distinguished only in the upper half of the flower. The styles are completely free. The ovules arise from the infolded carpel edges which form the placentae. The exposed surfaces of the carpels develop a very dense pubescence (plate 1).

During the development of the carpels the torus continues to grow, and thus elevates the stamens, petals, and sepals. The tip of the axis is below the carpels, and the placentae are carpel tissue only. Since the center of the torus does not undergo any growth, there is no central column of axis tissue extending up through the set of five carpels.

As the distal portions of the ovaries remain exposed and are not covered with receptacle tissue, the loquat flower is only partially epigynous. A photomicrograph of the developing floral parts is shown in plate 2.

OVULE DEVELOPMENT AND MACROSPOROGENESIS

Early in carpel development there occurs, slightly below the middle of each carpel, a growth of the placenta which develops into the ovule. Soon a second protuberance is seen—directly basal to the first—which becomes the obturator. Although the obturators are relatively large, their later growth does not keep pace with that of the ovules; at the time of full bloom the obturator is scarcely discernible to the naked eye.

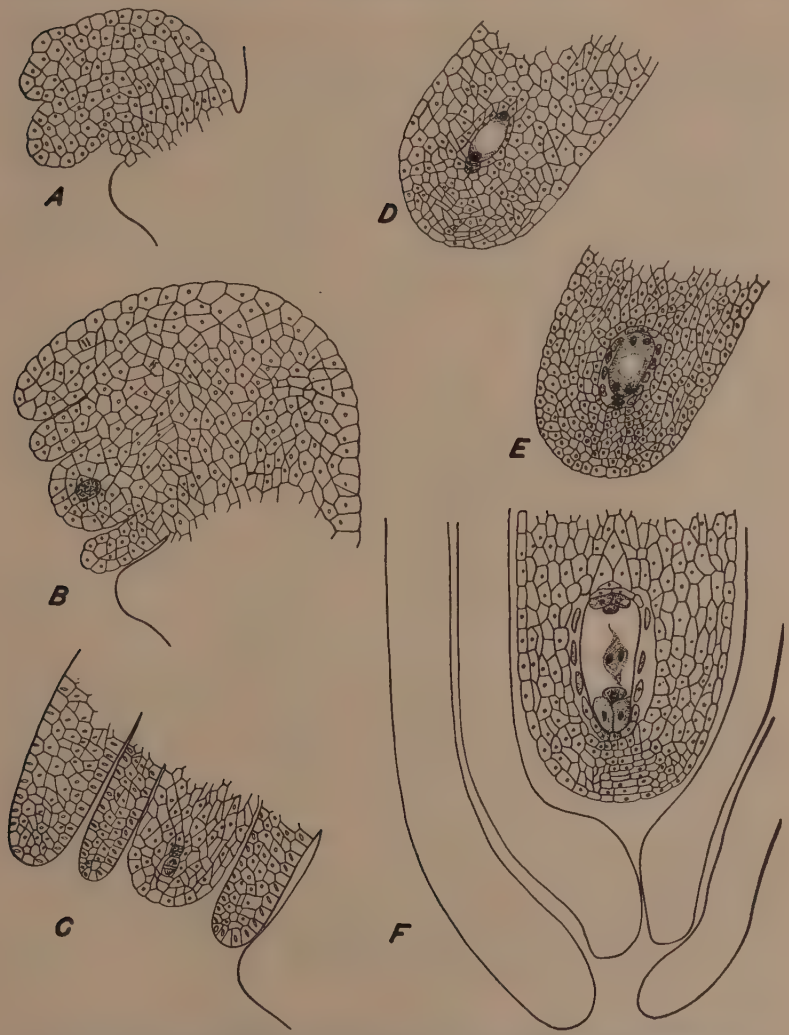


Fig. 3.—Macrosporogenesis in the loquat. *A*, Development of integuments; *B*, macrospore mother cell just before reduction division; *C*, formation of linear tetrad of macrospores; *D*, two-celled gametophyte and degenerating macrospores; *E*, four-celled gametophyte and degenerating nucellar cells, contiguous to embryo sac; *F*, mature macrogametophyte.

The two ovules in each carpel are usually side by side, one being slightly more elevated than the other. As growth of the young ovule continues, there is more cell division on one side than on the other, and soon the micropylar end points downward and outward toward the car-

pel wall, later becoming typically anatropous. At about the time when the ovule is at a right angle to the funiculus, first signs of the inner integument appear. From the epidermis of the ovule at a level just basal to a point where the macrospore mother cell will later develop arises the inner integument (fig. 3, *A*). Very soon thereafter the outer integument originates from the epidermal layer just basal to the point of origin of the inner integument. The outer integument grows somewhat faster than the inner; and, by the time the female gametophyte is fully developed, the integuments fully enclose the nucellus.

Soon after the appearance of the initials of the inner integument, the macrospore mother cell may be observed. Its origin was not noted although an archesporial cell was observed in a few instances. The macrospore mother cell usually lies two to four cells back from the micropylar end of the nucellus. Soon the macrospore mother cell undergoes heterotypic division. A chromosome plate in such a cell during heterotypic division is seen in figure 3, *B*. Thirty-two chromosomes were counted in this plate. To ascertain definitely the chromosome number, more such plates would be necessary. Moffett[6] has reported that root tips of the loquat had thirty-four chromosomes, and it is possible that two chromosomes were not visible in the plate counted. Loquat chromosomes are very small and are subject to clumping during fixation.

Heterotypic is followed immediately by homeotypic division, and a linear set of four macrospores is formed (fig. 3,*C*). The chalazal macrospore is functional, and the other three disintegrate (fig. 3, *D*). No irregularities could be seen in the formation of the eight-nucleate female gametophyte. During the development of the embryo sac there is a dissolution or breaking down of cells of the nucellus contiguous to the embryo sac. This dissolution process, which is concomitant with sac development, seems to allow for volume increase of the sac. A conspicuous feature of the nucellus when the mature female gametophyte is formed is a group of large, elongated cells at the chalazal end of the embryo sac (figs. 3, *E* and *F*).

Tetrads of microspores could be observed during the formation of the macrospore mother cell. When the linear tetrad of macrospores was formed, the microspores were still in the tetrad stage. During the formation of the two-celled macrogametophyte, pollen was observed in the anthers.

The curvature of the nucellus increases during the development of the macrogametophyte; and by the time the eight-nucleate state is attained, the ovule is completely anatropous. The micropylar end rests against the oburator.

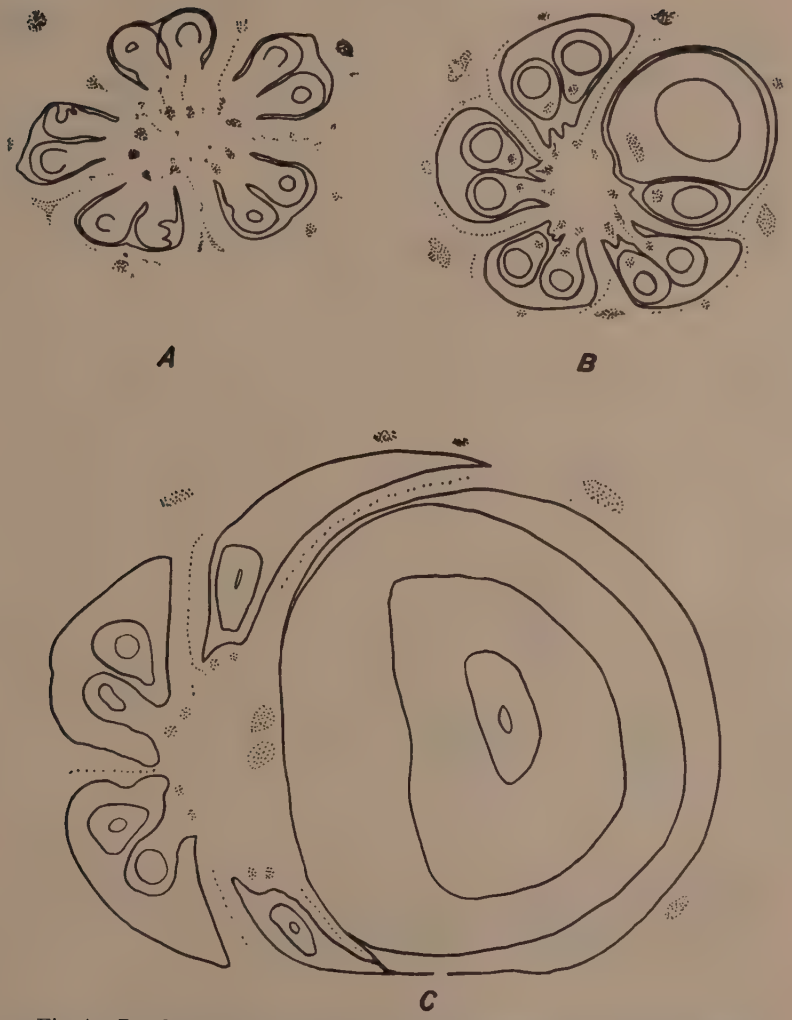


Fig. 4.—Development of seed in loquat and abortion of ovules. *A*, Ten potential seeds; *B*, initiation of abortion of nine ovules; *C*, seed and aborted ovules (note distortion of carpel walls due to growth by seed).

OVULE ABORTION

Apparently all ten ovules develop normal gametophytes. It was not discerned whether the eggs in all ten ovules are fertilized or not; however, in this variety only one or two ovules develop embryos. The cause of abortion of eight or nine ovules has not been determined. Climatic

influence on the nutritional status of the ovules may have some importance, however, since in the more southern portions of the state four or five seeds often develop in the variety Advance. In the ovules which failed to develop embryos the gametophytes remained apparently normal for several days and then degenerated. Two functional seeds seldom develop in the same carpel; but, where they do, one soon supersedes the other, and only one seed develops in the fruit. The functional seed or seeds develop very rapidly and soon distend the confines of their carpel so that the other carpels are distorted and compressed into a very small area. Degrees of abortion are illustrated in figure 4, *A*, *B*, and *C*.

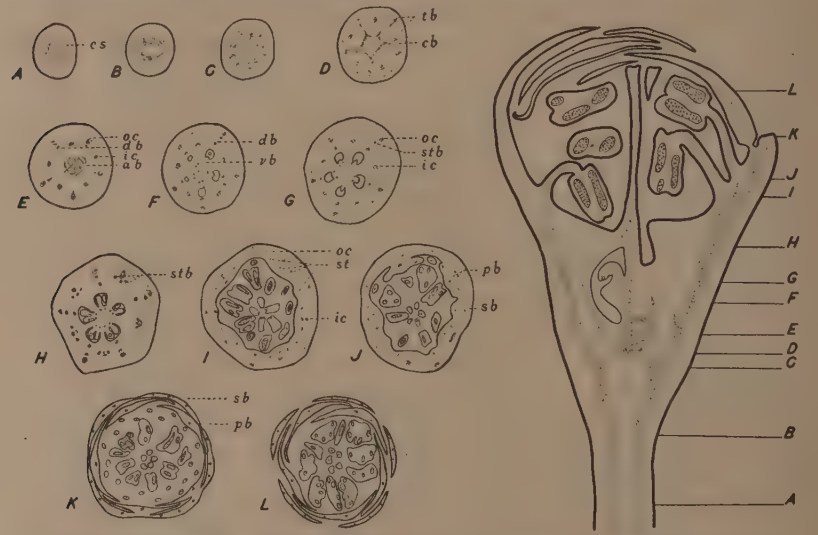


Fig. 5.—Vascular anatomy of loquat flower. Diagram on right shows levels at which depicted sections were cut. The parts are: *cs*, central stele; *cb*, central bundles; *tb*, toral bundles; *db*, dorsal bundles; *ab*, anastomosing bundles; *stb*, stamen bundles; *sb*, sepal bundles; *oc*, outer-cycle primary bundles; *ic*, inner-cycle primary bundles; *vb*, ventral bundles; *pb*, petal bundles.

VASCULAR ANATOMY OF FLOWER AND FRUIT

The vascular anatomy of a typical terminal flower is described in this report. Terminal flowers on the panicle have longer pedicels, and the method of bundle divergences is easier to trace in detail than in the pedicels of lateral flowers.

At the base of the pedicel the vascular cylinder is complete and more or less pentagonal (fig. 5,*A*). As it is traced up through the pedicel, however, it is seen to divide into ten distinct bundles (fig. 5,*B*). The exact point where this division occurs varies with different flowers, but is

usually about midway up the pedicel. The ten bundles diverge outward and are soon more or less equidistant, and the smaller bundles remaining between them diverge toward the median axis of the pedicel (fig. 5, *C*). These smaller bundles in the median portion form a star-shaped column just distal to the apex of the pedicel (fig. 5, *D*). The ten major bundles at this point form two cycles of five each, every alternate bundle being in the same cycle. At the apex of the pedicel they diverge into the toral region of the flower and follow the region between the pith and cortex.

Just basal to the carpels, the small bundles in the inner cylinder or median portion undergo extensive anastomosis and invade the central pith area to a considerable extent (fig. 5, *E*). This anastomosis continues to a level about even with the base of the carpels. Above this point the bundles become discrete. Two of these distinct small bundles extend up through each carpel and form the placental bundles of the flower. These ventral bundles furnish the vascular supply to the ovules and fuse before extending into the styles.

As has been stated, the ten primary or toral bundles follow the line of demarcation between the pith and the cortex. The bundles of the outer cycle are opposite the dorsal sutures of the carpels, and those of the inner cycle alternate with the carpels. At a level just below the bases of the carpels, five small bundles diverge from the outer cycle of toral bundles (fig. 5, *E*). All five do not branch from the primary bundles at exactly the same level. These five bundles (the dorsals) diverge toward the center of the flower, closely follow the dorsal sutures of the carpels, and then pass through the distal portions of the carpel walls and up into the styles (fig. 5, *F*). Thus there are fifteen main vascular bundles in the carpellary system—ten ventrals and five dorsals.

From each of the five primary bundles of the outer cycle arises one branch from the inner or pith side at a point on a level with the bases of the ovules (fig. 5, *G*). Although the exact point of origin of these branches varies, none branches at a point higher than at a level even with the median portion of the ovules. These five branches continue upward through the torus and terminate, one in each stamen of the inner cycle. At a point somewhat distal to the point of origin of the bundles that terminate in the inner stamen cycle, one bundle branches off from each of the inner cycle of primary toral bundles (fig. 5, *H*). These branches extend upward and terminate in the middle cycle of stamens. Slightly higher than the point of origin of the last-mentioned bundles, two more branches are given off from each of the inner cycle of primary toral bundles. These branches constitute the vascular supply of the outer cycle of stamens (fig. 5, *H*).

The petals derive their vascular supply from the inner cycle of primary bundles. After divergences for both the middle and outer cycle of stamens have been given off, each bundle of the inner cycle continues up through the cup-shaped torus (above the carpel level) and breaks into three separate bundles. The innermost of these three diverge into the petals, and the outer two extend into the sepals, as will be described later (fig. 5, *K*). The bundle extending into the petals forms the midrib and gives off branches to form a vascular network.

The sepals obtain their vascular supply from both the inner and the outer cycle of toral bundles. The median bundle or midrib of each sepal is the termination of one of the outer toral primary bundles. The small lateral bundles in the sepals are divergences from the inner primary bundles mentioned above. Following the divergences into the petals by one of the three bundles described in the foregoing paragraph, the second extends into a sepal to the right, and the third into the sepal to the left of the adjacent petal (fig. 5, *K*).

The cortex of the flower and fruit gains its vascular supply from branches from the ten primary toral bundles. These branches divide comparatively little until they reach the subepidermal region, where they branch and anastomose profusely, forming a network of fine bundles.

The vascular anatomy of the loquat resembles that of the apple as described by Kraus and Ralston[4] but differs in several respects. The anastomosis occurring in the median portion of the stele of the pedicel does not extend through so long a distance in the loquat as in the apple. Divergences for the stamen bundles occur at considerably lower levels in the loquat than in the apple.

DEVELOPMENT OF THE FRUIT

After fertilization, the loquat fruit develops very rapidly. The first indication of fruit enlargement is a thickening of the toral rim immediately above the carpel level. The whole toral region undergoes cell division and enlargement more or less uniformly throughout. The sepals grow toward the center and cover over in "hood" fashion the distal portions of the carpels. The sepal bases thicken and persist as permanent structures, whereas the petals, stamens, and styles dry up. The hood or cap enclosing the distal portions of the carpels may be excised from immature fruits, and the five carpels be exposed to view (plate 4, *A*). Remnants of the petals, stamens, and styles may be seen when this toral rim is cut off.

The toral rim of a number of fruits was removed on April 11, 1935, while the fruits were still on the tree. When the cut was made above the

carpels, the torus was almost completely regenerated, and the carpels were again hooded over; but whenever the cut pierced the carpel proper and cut a portion of the ovule, the fruits either died or ripened prematurely without attaining their full size.

The functional ovule develops into a fertile seed occupying the whole central region of the fruit; and the confines of the individual carpel walls which surrounded nonfunctional ovules are wholly disrupted (plate 3, *A* and *B*). The distal wall of the carpel in which the functional seed is found undergoes considerably more growth than do those of the other carpels. The result is an elevation of the distal wall of the carpel containing the functional ovule over those of the others.

By the time the fruit is mature, the carpel walls are more or less parchmentlike. The seed is extremely hard, the integuments and cotyledons being very resilient.

The skin of the mature fruit is comparatively tough, being more leathery than that of either the pear or the apple.

As has been indicated in the foregoing discussion, the edible portion of the loquat is entirely toral in nature, consisting of the pith and cortical areas. Development of the edible portion consists of a rather uniform growth of receptacle tissue throughout the fruit (plate 4, *C*). The toral cells of the mature fruit are large, thin-walled, and very juicy.

EFFECT OF LOW TEMPERATURES ON DEVELOPING LOQUAT FRUITS

Since the flowering period at Davis in the 1934–35 season was from the middle of October to February, the flowers and young fruits were subjected to comparatively low temperatures. The mean temperature of December was 48.3° F, and that of January, 45.8°; but the flowers not only were uninjured but were fertilized and developed into fruits during this period. Late in January the temperature on one night dropped to 29°. This resulted in an injury to many young fruits, thinning numerous panicles to one fruit. In nearly all cases, the terminal fruits persisted.

Many fruits injured by this cold period did not drop from the tree. In them the toral region became loosened from the carpels and could easily be "shelled" off. When the ovules of these injured fruits were not affected, these loosened areas tightened within a few weeks, and the fruits grew to normal size. The fruits that had injured ovules and yet did not drop never recovered from the injury to the torus; they grew very little in size thereafter and ripened prematurely.

SUMMARY

Floral development of the loquat (*Eriobotrya japonica*) is acropetal. The development of the floral organs is here described in detail. The loquat flower is semiepigynous and possesses ten ovules.

In the development of the macrogametophyte the macrospore mother cell undergoes heterotypic and then homeotypic division, resulting in the formation of a tetrad of macrospores. The chalazal macraspore only is functional, the remaining three disintegrating. As a result of three successive nuclear divisions, an eight-nucleate female gametophyte is formed.

Apparently normal macrogametophytes are formed in all ten ovules, but in the variety Advance only one or occasionally two seeds develop in each fruit at Davis, California.

The vascular anatomy resembles that of the apple, but the region of anastomosis in the stele of the pedicel is less extended than in the apple. Also, the point of divergence of the stamen bundles occurs at a considerably lower level in the loquat than in the apple.

The fruits have a hood or cap of toral tissue enclosing the distal portion of the ovary. This toral cap may be excised, and the distal portions of the carpels exposed to view.

The functional seed or seeds are fertile and occupy the whole central region of the fruit. Their development results in a marked distortion of the carpel walls and a complete dislocation of the nonfunctional ovules and the carpels in which they were located.

LITERATURE CITED

[1] Bailey, L. H.
Standard cyclopedia of horticulture. 6 vols. 3042 p. The Macmillan Company, N. Y. 1914.

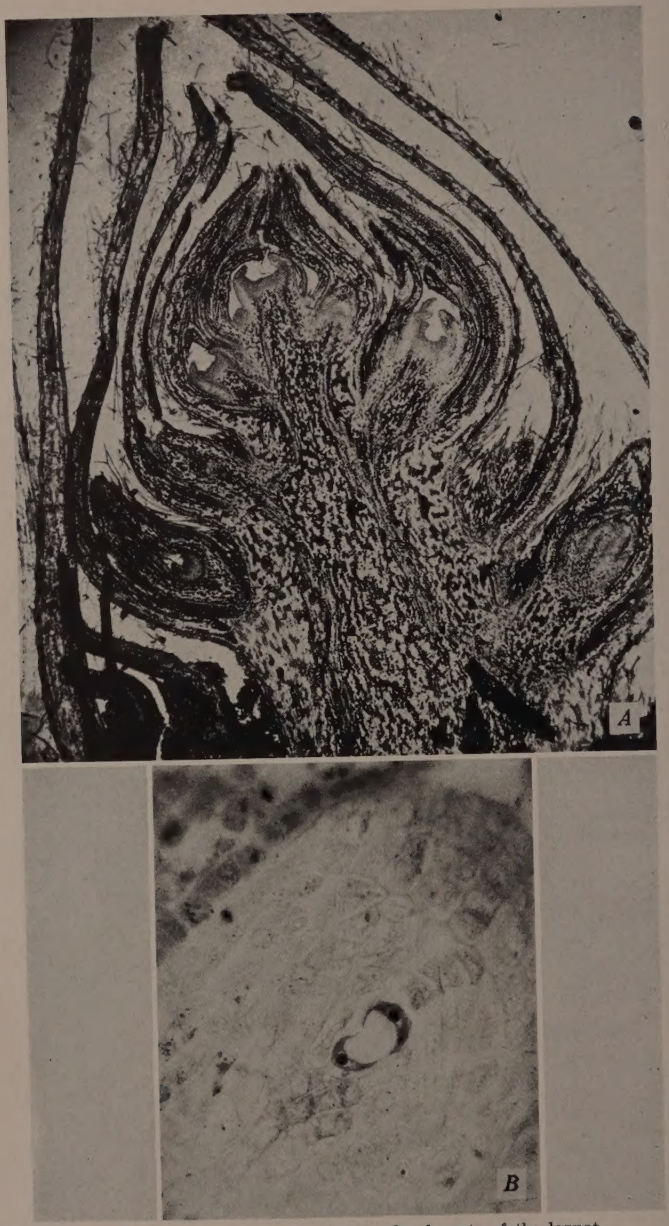
[2] Condit, I. J.
The loquat. California Agr. Exp. Sta. Bul. 250:251–284. 1915.

[3] De Zeeuw, R.
The value of double infiltration in botanical microtechnique. Papers Mich. Acad. Sci. 1:83–84. 1921.

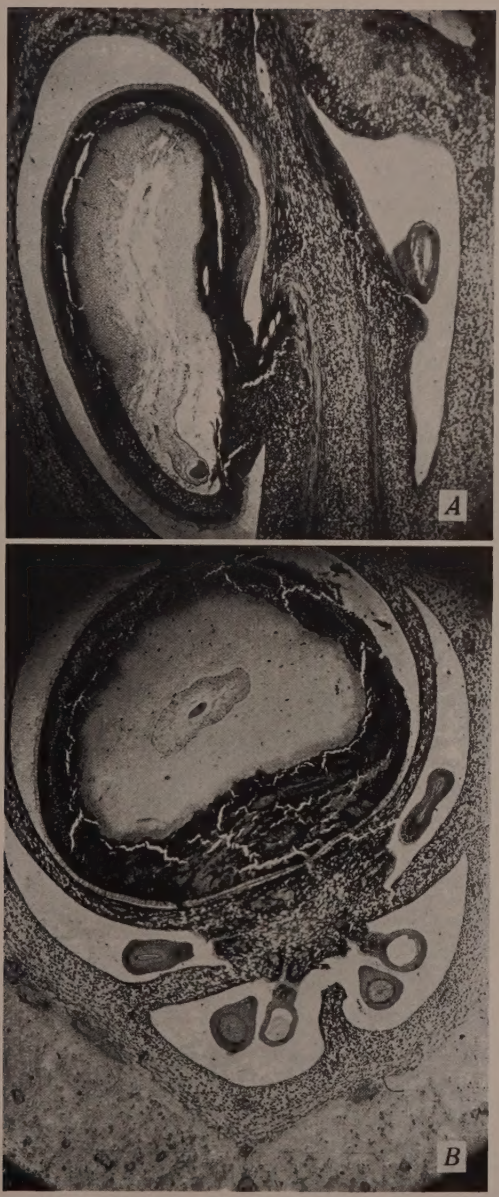
[4] Kraus, E. J., and G. S. Ralston.
The pollination of pomaceous fruits. III. Gross vascular anatomy of the apple. Oregon Agr. Exp. Sta. Bul. 138:1–20. 1916.

[5] Moffett, A. A.
The chromosome constitution of the Pomoideae. Proc. Royal Soc. Botany 108:423–446. 1931.

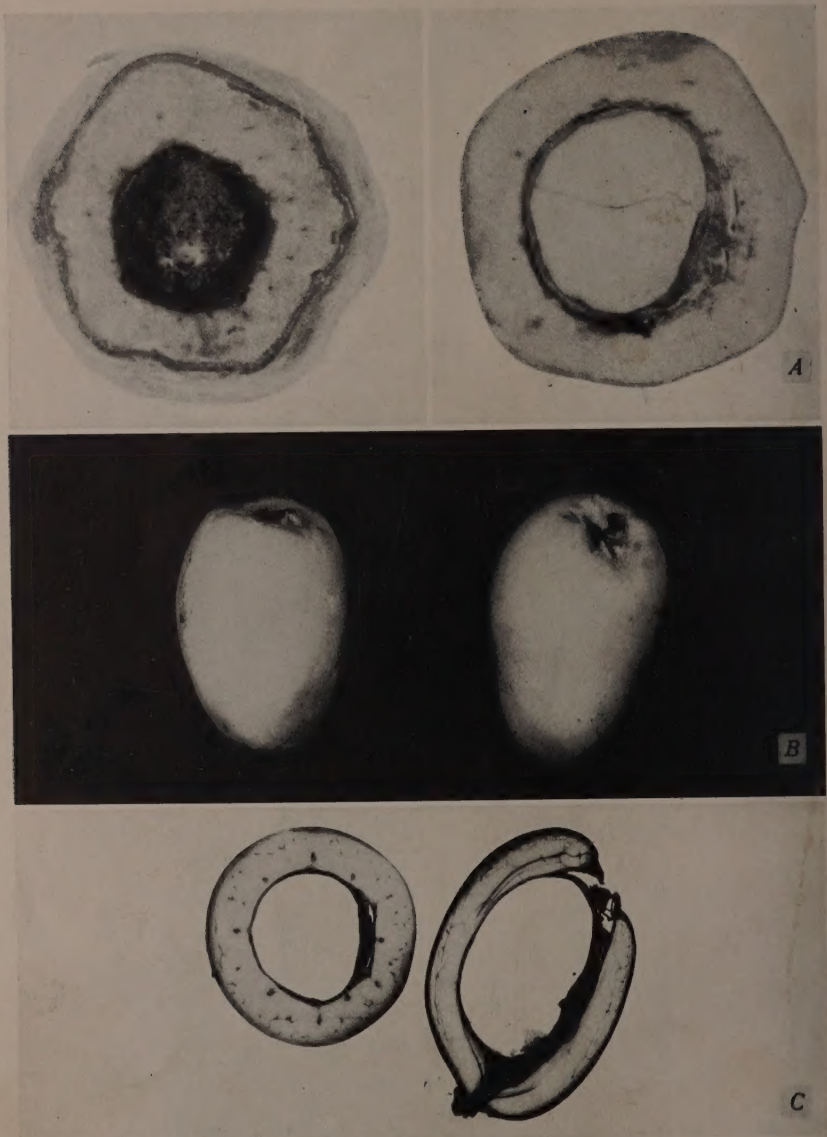
Photomicrograph of very young loquat flower. Note extreme hairiness of bracts and of the young flower.



A, Photomicrograph of developing floral parts of the loquat.
B, Photomicrograph of two-nucleate female gametophyte.



A, Photomicrograph of longitudinal section of young fruit, showing developing seed (at left) and aborting ovules (at right). *B*, Cross section of young fruit showing developing seed and aborting ovules.



A, In the fruit on the left, the toral rim has been excised to expose the carpels. The fruit on the right has been cut to show the seed and the distorted carpels. *B*, Mature loquat fruits of the Advance variety. These fruits are golden yellow. *C*, Cross and longitudinal cleared sections of loquat fruits. The seed has been removed in each case. The conspicuous and edible portion of the fruit is entirely toral in nature. The primary toral bundles in the cross section indicate the line of demarcation between pith and cortex. The compressed carpel walls may be seen in both sections.

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